THE BREEDING AND BEHAVIOUR OF MOCKINGBIRDS ON THE GALAPAGOS

by

Nicola Grant

Mockingbirds are commonly encountered on all the major islands of the Galapagos archipelago except Floreana. They did occur on Floreana as well but went extinct there in the latter half of the last century (Harris, 1973). There are four species of mockingbirds on the islands: *Nesomimus trifasciatus* (on Champion and Gardner — near Floreana), *N. macdonaldi* (on Española), *N. melanotis* (on San Cristóbal), and *N. parvulus* (on the remaining large islands).

They have been studied for short periods of time by Venables (1940), Hatch (1966) and S. Groves (unpubl.) (See also Abbott and Abbott, 1978). Because there is still so little known about their life histories and their breeding and feeding habits I initiated a project on *N. parvulus* on Isla Genovesa in January of 1978. My father and I studied the breeding, feeding and general behaviour of these birds from January until May (Grant and Grant, 1979). By banding the birds with colored rings we were able to identify different individuals. We returned to Genovesa in 1979, 1980 and 1982 from June to August. The project was also continued in March of 1979 and for the whole breeding season in 1980 by Margaret Kinnaird, and for the breeding seasons of 1981 and 1982 by Bob Curry.

During the breeding seasons we studied the social breeding of the mockingbirds and during the non-breeding seasons we concentrated on the activities of young birds and their family groups.

Two groups of Galapagos Mockingbirds displaying aggressively at a territorial boundary
Photo by Hendrik Hoeck

CO-OPERATIVE BREEDING

In 1978, by watching mockingbird nests every other day for four hours each day, I observed that at some nests three, and very occasionally four, individuals were bringing food to the nestlings. By banding nestlings at the nest I later discovered that 11% of the visits to the nest were made by the "helper" which was, in all but one case, the eldest son of the previous brood. Subsequent studies involving larger samples by Margaret Kinnaird and Bob Curry confirmed both observations, and also revealed that the helper may continue to help his parents rear his siblings for up to three years rather than attempt to breed himself.

Therefore the earlier suspicions of Hatch (1966) and S. Groves (pers. comm.) that the Galápagos Mockingbird is a co-operative breeder are correct. In general co-operative breeding is not common among birds, since usually only the parents raise their young, but de Vries (1975) has described another form of co-operation among Galápagos Hawks *(Buteo galapagoensis):* this is described in detail by Faaborg et al. (1980).

CONSEQUENCES OF THE HELPING BEHAVIOUR

Our combined studies of mockingbirds on Genovesa have shown that nests with help fledge more young than do those without help. However, helpers have no effect on the growth rate of the nestlings, although they do increase the total frequency of the nest visits. When there was a helper, the number of visits made to the nest by the father decreased while the female's work load remained unaltered.

During the non-breeding seasons (May through December) we have observed that the helpers are active participants in "flick-fights". "Flick-fights" are displays of aggression between family groups at territorial boundaries by the males and occasionally the females of a family group: they were first described by Venables (1940) for the mockingbirds *(N. melanotis)* on San Cristóbal, who referred to them as dances, and then described in more detail for all four species by Hatch (1966). The birds alternately crouch and straighten their bodies continuously flicking their wings and making a "chirrup" sound. Sometimes violent pecking and grappling with the feet ensues. The helpers are, however, always subordinate to both the mother and the father of the family group to which they belong.

THE COSTS AND BENEFITS OF HELPING AT THE NEST

Why do mockingbirds breed co-operatively? To try to answer this we have looked at the advantages and disadvantages to the helpers and to the parents (Kinnaird and Grant 1982). The advantages to the parents of having a helper at the nest are apparent. My study of the mockingbirds, Woolfenden's (1975) study of scrub jays in the USA and the Brown et al (1982) experimental study of babblers in Australia have all shown that the parents raise more young with helpers at a lower cost to the father. Possibly the mother also benefits by producing more offspring during her lifetime than she would otherwise, but our studies have not been going on for long enought to ascertain this: we still do not know the life expectancy of an average mockingbird.

The advantages to the helpers are not so obvious. W.D. Hamilton has suggested that an individual, by helping his parents rear his siblings, benefits by passing on a portion of his genes (in his brothers and sisters) to the next generation. By helping his parents to breed an individual also gains the experience of breeding without suffering any loss if the nestlings die.

It is possible that young male mockingbirds remain on their natal territory and help their parents rather than breed themselves because they have difficulty in establishing territories or gaining mates. From our observations in 1978 to 1982 we have found that: 1) mockingbird territories are close together, with no vacant spaces between them, and they are vigorously defended by flick-fighting during the non-breeding season. 2) The sex ratio is biased towards males. There are approximately one third more males than females on territories with breeding owners. 3) Adult breeding mockingbirds appear to be long lived because approximately a quarter of our banded adult mockingbirds in 1978 were alive and breeding in 1982. Thus relatively few new breeding opportunties exist each year. 4) New birds establishing territories either took the place of lost breeders or took a piece of their parent's territory. These four points indicate how difficult it is for a young bird to find a mate, set up a territory, and start breeding.

DISPERSAL AND THE UNEQUAL SEX RATIO

In point 2,I mentioned a sex bias in favour of males. Captures of mockingbird fledglings in May of a given year approximately one month after the end of the breeding season show the ratio of males to females to be almost 1:1. By the following breeding season, however, the ratio is 1.3:1 in favour of males. This inequality can partly be accounted for by the dispersal and high death rate of young females. While young males often remain on their natal territory to help their parents with the next brood, young females usually disperse. We have seen banded females wandering far from their natal territory. In July of 1982, there were nine females for every male that wandered, unbanded, into our study area.

Dispersing young birds entering a new territory squeak and display the submissive posture but are nevertheless chased out and occasionally vigorously attacked. However, in some instances, persistent intrusions by a young male or female have resulted in acceptance by the group. We have observed that females often return to their parental group during the non-breeding season after breeding far from their natal territory. As yet we do not know the reason for this behaviour.

The hazards of dispersal, i.e. attacks by territory owners and the poor chances of finding and holding a territory, may, in part, account for the loss of females, for presumbaly many dispersing birds die. Another reason for the unequal sex ratio may be that since helpers aid males more than females, females may put more effort into breeding and consequently may not live as long.

INBREEDING

Some authors (e.g. Greenwood, 1980) have suggested that the greater dispersal of one sex has evolved to avoid the disadvantages of inbreeding. Many ornithological studies have shown that it is usually the females that disperse furthest. Aggressive sibling rivalry between sisters and brothers, resulting in the departure of the sisters, may have been selected for to minimize the chances of inbreeding.
But inbreeding does occur. On Genovesa we have observed two cases. In the first instance an adult breeding male died and the helper bred with his mother. They produced two broods with three to four nestlings each in successive years. The young all died prior to fledging. The second case was a sister-brother mating when the sister did not disperse. They produced one brood from which all three nestlings fledged, but later all three disappeared.

N. TRIFASCIATUS ON CHAMPION ISLAND

On the little island of Champion-near-Floreana there are better opportunities to observe the effects of inbreeding. Champion is a circular island a quarter of a mile in diameter. It has a mockingbird population of between 40 and 50 individuals in about a dozen family groups.

The mockingbirds on Champion are of a different species than those on Genovesa. They are *Nesomimus trifasciatus* and the only other island on which they exist in Gardner-near-Floreana, another small island about 8 miles away from Champion. There appears to be no dispersal of *N. trifasciatus* between the two islands. Champion is, therefore, an ideal island on which to study inbreeding and its effects.

In August of 1980 my father and I measured and banded almost every bird on Champion and mapped the territory boundaries of the groups. We found less variation between the measurements of different individuals than between those on Genovesa, indicating that the Champion birds are closely related and rather inbred. Another possible indication of inbreeding is their behaviour. On Champion, as on Genovesa, territories were tightly packed together, but despite this, we saw no flick-fighting and very little aggressive behaviour, although Hatch (1966) did note four sightings of flick-fighting. This raises an unanswered question: Why is there little aggression *between* groups, which may be related, when there is typical dominant-subordinate aggression *within* groups, whose members are likely to be more closely related (for example, parents and offspring)?

FUTURE FIELD WORK

In the future it would be interesting to find out if there is a mechanism to minimize inbreeding, such as the recognition of parents, siblings, and cousins.

Bob Curry visited Champion in 1981 and 1982, but none of us has yet been on the island during the breeding season and therefore we do not even know if *N. trifasciatus*, like *N. parvulus*, is a social breeder. We strongly suspect that it is.

Our studies have only been going on for four years. In this amount of time we have not been able to answer many important and interesting questions. For example, it is important to find out if males have longer life spans than females. If they do it would support our observations that *N. parvulus* males benefit much more from the helper's assistance than do females, i.e. sons help fathers more than mothers. Some birds help their parents, instead of breeding themselves, until they are three years old. Are they more successful in rearing their own offspring than those who have never helped their parents? We have found that a small minority of the helpers do not appear to be related to those they help. Why then are they helping? Is this a sacrifice they make to increase their own chances of breeding at a later date?

Eventually, by answering these and similar questions, it will be possible to compare the breeding strategies and success rates of all four species of Galapagos mockingbirds, and then to interpret the differences in terms of the different environmental conditions they are subjected to on the various islands.

REFERENCES

Abbott, I. & L.K. Abbott. 1978. Multivariate study of morphological variation in Galapagos and Ecuadorian mockingbirds. Condor 80: 302-308.

Brown, J.L., E.R. Brown, S.D. Brown & D.D. Dow. 1982. Helpers: effects of experimental removal on reproductive success. Science 215: 421-422.

de Vries, T. 1975. The breeding biology of the Galapagos Hawk, *Buteo Galapagoensis*. Le Gerfaut 65: 29-57.

Faaborg, J., T.J. de Vries, C.B. Patterson & C.R. Griffin. 1980. Preliminary observations on the occurrence and evolution of polyandry in the Galápagos Hawk *(Buteo galapagoensis)*. Auk 97: 581-590.

Grant, P.R. & N. Grant. 1979. Breeding and feeding of the Galápagos mockingbird, *Nesomimus parvulus*. Auk 97: 227-244.

Greenwood, P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Anim. Behav. 28: 1140-1162.

Harris, M.P. 1974. A Field Guide to the Birds of Galapagos. Collins.

Hatch, J.J. 1966. Collective territories in Galapagos Mockingbirds, with notes on other behaviour. Wilson Bull. 78: 198-206.

Kinnaird, M.F. & P.R. Grant. 1982. Co-operative breeding by the Galapagos Mockingbird, *Nesomimus parvulus*. Behav. Ecol. Sociobiol. 10: 65-73.

Venables, L.S.A. 1940. Nesting behaviour of the Galapagos Mockingbirds. Ibis 4: 629-639.

Woolfenden, G.E. 1975. Florida scrub jay helpers at the nest. Auk 92: 1-15.